# Aluminum tolerance in triticale, wheat, and rye *

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## Summary

Acid soils containing high levels of aluminum (Al) are known to severely limit plant growth on over 1.6 billion hectares worldwide. In the United States, a gradual decline in the pH of many soils both in the Great Plains as well as the Southeast, has caused many soils to become high in levels of free Al. This worldwide condition encouraged the analysis of wheat (*Triticum aestivum* L. em Thell.), triticale (X *Triticosecale* Wittmack), and rye (*Secale cereale* L.) germplasm from one of the major acid soil regions of the world (Brazil) in order to evaluate and compare the genetic potential of Al genes for cereal improvement. The objectives were to compare Al-tolerance levels in wheats, triticales, and ryes by measuring root elongation responses in Al-containing hydroponic nutrient solutions. Root elongation was impaired for all species grown in 1 mg/L concentrations of Al. Rye had the longest root regrowth and Al-sensitive wheats had the shortest root regrowth. The triticales containing a 2D(2R) substitution developed in the mid-1970s had the poorest root regrowth of all triticale types. The newly developed advanced triticale lines (AABBRR) yet to be released for commercial production showed the highest degree of Al tolerance of all the triticale types and approached or exceeded the levels observed in rye. This indicated that progress is being made in improving Al-tolerance of triticale in Brazil. Of all the old and new wheat varieties showing the highest degree of Al-tolerance, none of them were better than 'BH 1146' a variety that is at least 50 years old. This indicated that over the past 50 years, although Brazilian wheat breeders have made yield improvements in wheat production, they have not improved Al-tolerance. Rye showed a higher degree of Al-tolerance than the other cereals when tested in 1 mg/L of Al, but as expected, some variation was noted.

## Introduction

With the worlds population currently over 6 billion and currently growing at rate of about 1.9 to 3.9% per year (depending on the country involved), it is clear that existing agricultural production need to accelerate in order to keep up with population growth and an ever increasing demand for food. The United Nations has indicated that agricultural production will have to increase approximately 66% by 2040. Therefore, not only is a tremendous increase in food production on existing soils needed, but also new land under cultivation will be needed in order to meet the increase in food demand. The United Nations Food and Agricultural Organization has indicated that the last major land masses that can potentially be converted into agricultural production are the acid soils of the world (for example: those of the Cerrado in Brazil and the Llanos of Colombia and Venezuela).

Acid soils are known to severely limit plant growth on about 1.6 billion hectares worldwide, which represents roughly 49% of all arable land (Granados et al., 1993). A reduction in the use of liming has resulted in a further lowering of soil pH and increased aluminum (Al) toxicity, thus limiting production in many traditional wheat producing areas and the expansion of wheat production into nontraditional areas (Carver et al., 1988; Briggs & Taylor, 1994). The development of new cultivars with increased Al-tolerance under both favorable and unfavorable environments is regarded as a fundamental and economic solution to helping increase world food production. Increased Al-tolerance should also make liming and fertilization more cost effective (Foy et al., 1965; Foy & da Silva, 1991; Ruiz-Torrez et al., 1992; Granados et al., 1993; Briggs & Taylor, 1994). The value of using Al-tolerant cultivars is clearly evident from comparing near isogenic lines of wheat that differed in Al-tolerance; 31% more spikes, 66% more biomass, and 68% higher grain yield were obtained when Al-tolerant lines were grown on acid soil (Carver et al., 1993).

Species and genotypes within species are known to differ widely in their tolerance to Al (Foy et al., 1974; Little, 1988; Aniol & Gustafson, 1990; Rajaram et al., 1991). Acid-soil and/or Al-tolerance has been identified in wheat (*Triticum aestivum* L. em Thell.) (Foy et al., 1965; Mesdag & Slootmaker, 1969; Taylor & Foy, 1985; Carver et al., 1988; Foy & da Silva, 1991; Nyachiro & Briggs, 1994; Aniol, 1995; Luo & Dvorak, 1996), and triticale (X *Triticosecale* Wittmack) and rye (*Secale cereale* L.) (Aniol et al., 1980; Camargo & Felicio, 1984; Camargo et al., 1991; Aniol, 1996) genotypes from various origins. Aniol et al. (1980) concluded that Al tolerance in rye inbred lines ranged between the Al-tolerant and Al-sensitive wheat cultivars. However, Camargo & Felicio (1984) reported that many rye cultivars tolerated significantly higher levels of Al in nutrient solution, than the Al-tolerant wheat and triticale cultivars.

Triticale germplasm containing a complete genome of rye chromosomes (AABBRR) has been shown to possess better adaptation and yield potential in marginal environments (Rajaram et al., 1993). Many so-called 'complete' triticales showed Al-tolerance levels closer to wheat than rye (Gustafson & Ross, 1990). This is an indication that the expression of the genes in rye controlling Al tolerance appears to be somewhat suppressed when in a wheat background. It is implied that the improvement of Al tolerance in triticale may be achieved by either increasing the expression of rye Al tolerance gene(s), or by selecting increased Al tolerance in rye followed by combining the highly Al-tolerant ryes with Al-tolerant wheats.

The objectives of the current study were to evaluate the levels of Al tolerance in different triticale and wheat genotypes from Brazil and to compare the results to that of known rye genotypes using a simple and rapid screening technique utilizing Al-containing hydroponic solutions. The results of this evaluation will be related to progress being made in breeding Al-tolerant Brazilian wheats and triticales.

## Materials and methods

### Germplasm

The germplasm used in this study included 2 rye, 19 triticale, and 9 wheat genotypes all from Brazil (Dr A.C. Baier, EMBRAPA, Passo Fundo, Brazil) as well as 1 rye cultivar from Poland and 1 rye landrace variety from Ecuador courtesy of the USDA-Sears collection (Table 1). The Brazilian triticale genotypes were comprised of three groups: (1) hexaploid triticales cultivars not containing a complete rye genome, but containing a 2D(2R) substitution that were developed prior to 1980 for production in Brazil; (2) hexaploid triticale cultivars containing a complete rye genome (AABBRR) with no substitutions that were developed between 1980 and 1985 for cultivation in Brazil; and (3) advanced hexaploid triticale lines containing a complete rye genome (AABBRR) currently being evaluated in field trials for release in Brazil. The hexaploid wheat cultivars were comprised of two groups containing of both old and modern cultivars grouped according to their Al-tolerance: (1) sensitive; and (2) tolerant based on replicated field trials conducted on acid soils in Brazil.

### Aluminum stress and analysis

Seeds of each genotype were placed on moist filter paper in Petri dishes, held at $2 \pm 1$ °C for 12 h and were then germinated for 24 h at room temperature. Six seedlings of each genotype with similar root lengths (3 to 10 mm) and comparable endosperm sizes were selected in order to eliminate any variation in the results due to endosperm or root length differences at the start of the study. The selected seedlings were placed on plastic mesh floating on 2 L of an aerated, low ionic strength hydroponic medium [400 $\mu$m $CaCl_2$; 650 $\mu$m $KNO_3$; 250 $\mu$m $MgCl_2$; 10 $\mu$m $(NH_4)_2SO_4$;

*Table 1.* Germplasm types, genotypes, pedigrees and the classification in to which each genotype was included

| Germplasm type genotype (cultivar) | Pedigree |
|---|---|
| **Al-sensitive wheat cultivars** | |
| Anahuac 75 | II 12300//LR 64/7C/3/NOR 67 |
| IAPAR 30 | ALD Sib//CNT 7/PF 70354/3/ PAT 24//BB//KAL |
| **Al-tolerant wheat cultivars** | |
| Trigo BR 43 | PF 833007/Jacui |
| Trigo BR 35 | IAC 5*2/3/CNT7*3/LD//IAC5/HAD |
| EMBRAPA 15 | CNT 10/BR 35//PF 75172/Tifton |
| Trigo BR | 23CC//ALD/3/IAS54-20/COP//CNT 8 |
| CNT 1 | PF 11.1000.62/BH 1146 |
| Trigo BR 37 | Mazoe/F 13279//Pelado Marau |
| IAC 5-Maringa | Frontana//Kenya 58/Ponta Grossa 1 |
| BH 1146 | Ponta Grossa 1//Fronteira/Mentana |
| **Substituted (2D/2R) triticale cultivars** | |
| Triticale BR 1 | M2A/CML (Panda) |
| Triticale BR 2 | FS 3972-48M-0N-0Y-0F |
| CEP 18 | TOB/8156//CC/3/Inia/4/SPY/5/M2A (Teddy) |
| IAPAR 13-Araucaria | M2A/CML//FN |
| **Complete triticale cultivars** | |
| Triticale BR 4 | BGL/CIN//MUS |
| EMBRAPA 17 | BGL/3/MTZTCL/Trigo//BGL/4/Nutria (Tatu) |
| EMBRAPA 18 | Tapir/Yogui//2*MUS |
| CEP 22 | BGL/CIN//IRA/BGL |
| CEP 23 | BGL/3/MTZTCL/Trigo//BGL/4/Nutria (Tatu) |
| CEP 25 | B6712-171-11Y-4Y-0M-0A |
| IAPAR 23-Arapoti | CIN/CNO//BGL/3/Merino (Hare) |
| IAPAR 38-Araruna | JLO/Panther |
| OCEPAR 3 | CIN/CNO//BGL/3/Merino (Hare) |
| **Complete triticale advanced lines** | |
| PFT 8922 | MUS/Lynx//Yogui/3/MUS |
| PFT 104 | Tatu*2/China 7 |
| PFT 107 | Hare 263/Civet |
| PFT 222 | LT-1/Rhino |
| TCEP 878 | Hare 263/Civet |
| PR 884 (IAPAR54, OCEPAR4) | B6811-270-27Y-3Y-0M (Uron) |
| **Rye genotypes** | |
| Blanco | (Brazilian, selected for Al 5 cycles at U of M) |
| Centeio BR 1 | (Cultivar from Brazil) |
| Dankowskie Zlote | (Cultivar from Poland) |
| Ecuador | (Landrace from Ecuador) |

40 $\mu$m $NH_4NO_3$ (pH 4.0)] containing Al (modified from Moore et al., 1976; Aniol, 1991). The Al was added as $AlCl_3$ to the acidified hydroponic medium at concentrations of 0.5, 1.0, 2.0, and 4.0 mg Al/L (mg/L= 37 $\mu$m of Al). A 'zero Al' control was also included for each genotype. The solution pH was adjusted to 4.0 ± 0.02 with HCl prior to, and with KOH, after the Al was added. No precipitation was observed in any of the solutions. The hydroponic tanks and seedlings were placed in a controlled environment (26 °C ± 1 °C 16 h day/8 h night) with a photon flux density of 1000 mmol $m^{-2}s^{-1}$. Seedling growth continued for 4 days with the solutions being changed each day in order to minimize potential changes in the pH and Al concentration.

The two longest roots from the 6 seedlings for each of two replications were measured and averaged for each genotype treatment and for all genotypes within a germplasm type. The root tolerance index (RTI) of each germplasm type and genotype was calculated by dividing the average root length in each Al concentration by the average root length in the solution with no Al (Taylor & Foy, 1985). Genotypes, as sub-plots, were randomized within each of two replications. Analysis of variance using a split-plot design was performed with germplasm type as the whole-plot factor and genotypes as the sub-plot factor.

It was previously determined that 1.0 mg/L Al produced the highest correlation between root growth and established acid-soil-tolerance levels (Baier et al., 1996). Therefore, average root length and RTI values of the germplasm types and genotypes in the solutions containing 0.5 mg and 1.0 mg/L Al were compared by Fisher's LSD.

## Results

The 19 triticale, 9 wheat, and 4 rye cultivars were utilized to evaluate the Al tolerance levels, under hydroponic conditions, of triticales relative to wheat and rye, and to compare the results to previously conducted field trials. For this purpose, the differences for root elongation and RTI among Al concentrations, germplasm types (GT) for triticale, wheat, and rye, GTxAl interaction, GT (1 mg/L Al), and cultivars (CT) were measured. The mean square differences in both root length and RTI for GT, GTxAl, and GT in 1.0 mg/l Al were all highly significant ($p = 0.001$).

Root elongation of all genotypes was reduced in the lowest concentration of Al (0.5 mg/L), but the de-
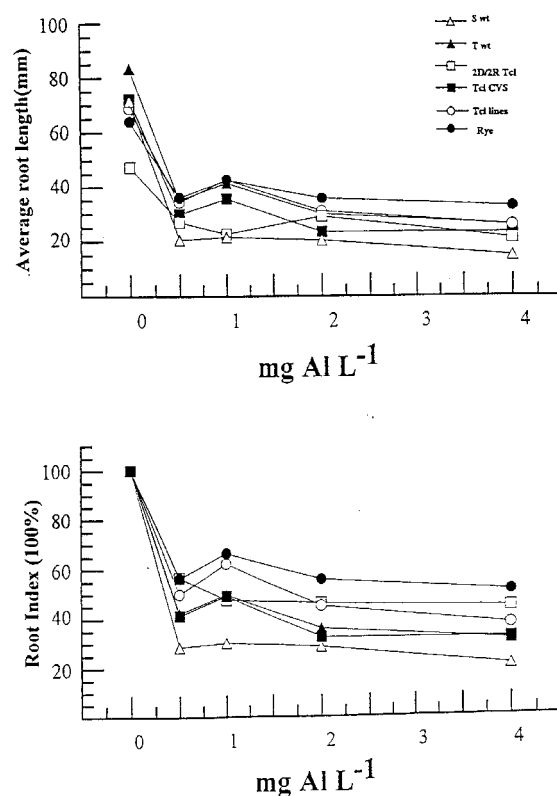


*Figure 1.* A. Root elongation of wheat, triticale, and rye germplasm types in various concentrations (mg/L) of Al-containing hydroponic solutions. Six seedlings of each genotype were grown for 4 d in hydroponic solutions. The average root length of each germplasm type was derived by averaging the two longest root measurements of all seedlings from each genotype within each germplasm type over two replications. Al-sensitive wheat cultivars, Al-tolerant wheat cultivars, substituted triticale cultivars, complete triticales, advanced triticale lines, and rye cultivars. B. Root tolerance index (RTI) of wheat, triticale, and rye germplasm types in various concentrations (mg/L) of Al-containing hydroponic solutions. Six seedlings of each genotype were grown for 4 d in hydroponic solutions. The RTI of each germplasm type was derived by averaging the two longest root measurements of all seedlings from each genotype within each germplasm type and two replications from the control solutions. Then dividing that by the two longest root measurements of all seedlings from each genotype within each germplasm type over two replications in various Al-containing hydroponic solutions. Al-sensitive wheat cultivars, Al-tolerant wheat cultivars, substituted triticale cultivars, complete triticales, advanced triticale lines, and rye cultivars.

gree of reduction in root length varied among the GT and the cultivars within the GT (Figure 1A; Table 2). The root growth in the control solution was not figured in any statistical analysis as it is obvious from Table 2 that any amount of Al suppresses root growth of all species to some degree. In the control solution containing no Al, the Al-tolerant wheats had the longest

*Table 2.* Analysis of variance of root length and RTI values following 4D growth in different Al concentrations in hydroponic solutions for wheat, triticale and rye genotypes

| Source of variation | df | Mean squares root length | df | Mean squares RTI |
|---|---|---|---|---|
| Replication (Rep) | 1 | 103.9 | 1 | 72.9 |
| Al | 4 | 18020.8** | 3 | 2653.3** |
| Rep × Al (error A) | 4 | 30.6 | 3 | 28.6 |
| Germplasm type (GT) | 5 | 1753.6** | 5 | 2508.7** |
| Germplasm type × Al | 20 | 304.8** | 15 | 142.2** |
| GT (1 mg Al L-1) | 5 | 729.4** | 5 | 823.9** |
| Cultivars (CT) | 27 | 799.0** | 27 | 934.0** |
| Cultivars × Al (GT) | 108 | 196.2** | 81 | 132.8** |
| Cultivars (1 mg Al L-1) | 27 | 223.5** | 27 | 934.6** |
| Error | 160 | 23.7 | 128 | 37.2 |

** Significant at $p = 0.01$.

roots, and the complete triticales and the Al-sensitive wheats had the second longest roots. The substituted triticales had the shortest roots of all the germplasm types. Rye showed an intermediate root length in the control solution as compared to the wheats and triticales. However, considerable variation was observed within.

Al-sensitive wheats had the shortest roots in the 1mg/L Al solution. The Al-sensitive wheats were completely separated from all other wheats and/or triticales in Al-containing solutions (Figure 1A and 1B). The average root lengths of the Al-sensitive wheats, the Al-tolerant wheats, the substituted triticales, the complete triticales, the advanced triticale lines, and the ryes were 21.6 mm, 42.2 mm, 22.6 mm, 35.6 mm, 42.9 mm, and 42.7 mm in 1.0 mg/L Al, respectively (Table 2). The Al-tolerant wheats, the advanced triticale lines, and the ryes showed the highest degree of Al tolerance by having the longest root growth in the 1.0 mg/L Al solution, while the group of Al-sensitive wheats and the group of substituted triticales showed the lowest degree of tolerance to the 1.0 mg/L Al solution when compared to the other wheat and triticale groups.

In the 1.0 mg/L Al solution, average RTIs of the Al-sensitive wheats, the Al-tolerant wheats, the substituted triticales, the complete triticales, the advanced triticale lines, and the ryes were 37.3%, 48.4%, 47.6%, 49.2%, 62.4%, and 50.6%, respectively (Table 2). The advanced triticale lines and the ryes were not significantly different in their degree of Al tolerance at 1.0 mg/L, while the Al-sensitive wheats showed the

lowest degree of Al tolerance. The Al-tolerant wheats and the substituted and complete triticales were not significantly different in terms of Al tolerance in 1.0 mg/L Al.

The recently developed advanced triticale lines had the longest roots and the best RTI as compared with the two other triticale types (Figure 1A; Table 2). The RTIs of the advanced triticale lines did not differ significantly from that of rye in both 0.5 and 1.0 mg/L Al.

Since Al-tolerance based on RTI expresses root growth relative to non-Al-containing solutions, as compared to total root growth following germination, the RTI values more accurately indicate a plant's ability to tolerate Al and continue root growth. The RTI values for the ryes, known to have a high degree of Al tolerance, and Al-sensitive wheats showed that they were clearly separated from all other germplasm types (Table 2). The substituted triticales had a slightly lower RTI than, but the difference was not significant, did the complete triticales, and both were significantly lower than the newly-developed advanced triticale lines Figure 1B; Table 2).

The degree of variation in Al tolerance among all genotypes in wheat, triticale, and rye was large and resulted in three distinct significantly different groups (Table 2). The complete triticale line 'IAPAR 38-Araruna' had the largest RTI (100.0) of all 33 genotypes studied at the 1.0 mg/L level of Al. While wheat 'BH 1146' with an RTI of 54.0 and rye 'Dankowskie Zlote', originally from Poland, with an RTI of 67.9 had the longest RTIs of the wheat and rye groups, re-

*Table 3.* Average root lengths and RTI values of germplasm types and genotypes grown 4 days in 0.5 mg and 1 mg/L aluminum including control

| Germplasm type | Control | Root length (mm) | | RTI (%) | |
| --- | --- | --- | --- | --- | --- |
| | | 0.5 mg/LAl | 1 mg/LAl | 0.5 mg/LAl | 1 mg/LAl |
| **Sensitive wheats:** | 71.6 | 20.5A | 21.6A* | 37.4A | 37.3A |
| Anahuac 75 | 29.0 | 15.0a | 14.3a* | 51.7 | 49.3 |
| IAPAR 30 | 114.3 | 26.0b | 29.0b | 22.8 | 25.4 |
| **Tolerant wheats:** | 86.6 | 35.2C | 42.2C | 41.0AB | 48.4B |
| TrigoBR 43 | 80.3 | 37.8cd | 37.0bc | 47.0 | 46.1 |
| TrigoBR 35 | 84.0 | 39.8cd | 39.0c | 47.3 | 46.4 |
| TrigoBR 23 | 78.8 | 31.0bc | 34.5bc | 39.4 | 43.8 |
| BH 1146 | 114.8 | 43.0cd | 62.0de | 37.5 | 54.0 |
| CNT 1 | 84.5 | 33.8bc | 37.8bc | 39.9 | 44.7 |
| IAC5-Maringa | 93.0 | 30.3bc | 49.3c | 32.3 | 53.0 |
| TrigoBR 3 | 70.8 | 31.0bc | 35.8bc | 43.8 | 50.5 |
| **Subtituted triticales:** | 47.5 | 27.0B | 22.6A | 57.3C | 47.6B |
| TriticaleBR 1 | 31.8 | 19.8ab | 14.0a | 62.2 | 44.0 |
| TriticaleBR 2 | 48.5 | 27.0bc | 25.0b | 55.7 | 51.5 |
| CEF 18 | 58.0 | 34.0bc | 24.3b | 58.6 | 41.9 |
| IAPAR 13-Araucaria | 51.8 | 27.3bc | 27.3b | 52.7 | 52.7 |
| **Complete triticales:** | 72.3 | 29.9B | 35.6B | 47.1B | 49.2B |
| TriticaleBR 4 | 55.8 | 32.3bc | 28.8b | 57.8 | 51.6 |
| EMBRAPA 17 | 53.0 | 36.5c | 31.5bc | 68.9 | 59.4 |
| EMBRAPA 18 | 107.0 | 25.2b | 40.3bc | 23.8 | 37.7 |
| CEP 22 | 37.0 | 32.3bc | 23.0b | 87.2 | 62.2 |
| CEP 23 | 77.0 | 25.8b | 36.0bc | 33.4 | 46.8 |
| CEP 25 | 100.5 | 32.3bc | 33.3bc | 32.1 | 33.1 |
| IAPAR 23-Arapoti | 90.3 | 31.3bc | 37.0bc | 34.6 | 41.0 |
| IAPAR 38-Araruna | 40.3 | 19.8ab | 40.3c | 49.1 | 100.0 |
| OCEPAR 3 | 90.0 | 33.3bc | 50.3d | 36.9 | 55.9 |
| **Advanced triticales:** | 68.8 | 34.4C | 42.9C | 55.8C | 62.4C |
| PFT 8922 | 43.8 | 41.5c | 40.9c | 94.9 | 93.4 |
| PFT 104 | 45.0 | 22.5ab | 21.0ab | 50.0 | 46.7 |
| PFT 107 | 54.0 | 40.0cd | 37.0bc | 74.1 | 68.5 |
| PFT 222 | 79.5 | 36.3c | 39.3c | 45.6 | 49.4 |
| TCEP 878 | 102.5 | 33.0bc | 63.3e | 32.2 | 61.8 |
| PR 884 | 87.8 | 33.3bc | 56.3de | 37.9 | 64.1 |
| **Ryes:** | 64.1 | 36.1C | 42.7C | 57.3C | 50.6C |
| Blanco | 88.8 | 46.3d | 55.0cde | 52.1 | 61.9 |
| CenteioBR 1 | 62.5 | 37.3cd | 48.0cd | 59.6 | 48.0 |
| Dankowskie Zlote | 66.0 | 36.3cd | 44.8cd | 54.9 | 67.9 |
| Ecuador | 93.3 | 24.5ab | 23.0ab | 62.4 | 24.7 |

* Averages of germplasm types followed by the same uppercase letter or averages of genotypes in all germplasm types followed by the same lowercase, do not differ by Fishers Protected LSD ($p = 0.05$).

spectively, in 1.0 mg/L level of Al. The Al-tolerance classes also showed variation within germplasm types for root length and RTI (Table 2).

## Discussion

The germplasm evaluated represents a broad spectrum of old and modern cultivars present in triticale, wheat, and rye germplasm and cultivars currently being grown for production in Brazil. Both the triticales and wheats showed significant variation in response to Al in the hydroponic solutions (Table 2). The Al-sensitive wheats were clearly separated from other wheats, triticales, and ryes in response to Al.

The wheats were separated into the two groups, sensitive and tolerant, based on their known agronomic performance under field conditions in Brazil. The data indicated that 0.5 mg/L Al was not sufficient a concentration of Al to differentiate the Al-tolerance levels in wheat cultivars. However, an Al concentration of 1.0 mg/L was sufficient to separate the wheat groups giving the same rankings as the results observed in the field evaluations. The data showed that BH 1146 is still the most tolerant wheat in Brazil. This occurs in spite of the fact that BH 1146 has been a commercial cultivar in Brazil for over 50 years. This indicates that even though Brazilian wheat breeders have made significant progress in increasing wheat yields in the past 50 years, they have not germplasm to inter-cross into their programs that has improved on existing levels of Al tolerance. This suggests that there might not be any more wheat genes available for increasing Al tolerance in the Brazilian wheat breeding programs. Since BH 1146 is also the most Al-tolerant spring wheat, so far screened, in the world (A. Aniol, pers. comm.), there might not be any additional un-utilized Al genes in the worlds spring wheat germplasm for further wheat improvement in order to increase production on more acid soils. This has implications for expanding world wheat acreage into more marginal acid soils (for example, those of the Cerrado in Brazil and the Llanos of Colombia and Venezuela) in order to increase production.

The triticales were placed into three groups depending on age of the cultivar and chromosome composition in order to compare the cultivar/genotypes from different periods of time in the Brazilian breeding programs. On the whole, average root lengths of the three triticale groups, when stressed with Al, were intermediate between the sensitive wheats and highly-tolerant ryes. However, there were significant differences between the triticale groups. The average RTI of the advanced triticale lines was not significantly different from that observed in rye when stressed in an Al solution of 1.0 mg/L. The complete triticales produced in the mid-1980s had intermediate RTIs between the advance triticale lines and the substituted triticale cultivars released for commercial production before 1980. There was no significant difference between the RTIs of the substituted and complete triticale groups when tested in 1 mg/L Al. The advanced triticale lines had significantly larger RTIs than the other two triticale groups when stressed in an Al solution of 1.0 mg/L. This indicated that Brazilian triticale breeders have not only been improving yield and other agronomic traits between the mid-1970s to the 1990s, but they have also been gradually improving the level of Al tolerance in triticale beyond that observed in the most Al-tolerant wheat cultivar. The results indicate that the improved Al tolerance levels in triticale are coming from genes present in the rye genome of hexaploid triticale and not the genomes of wheat.

This is consistent with observations by Rajaram et al. (1993) who considered that triticale germplasm with a full complement of rye chromosomes showed better adaptation and yield potential in marginal environments in replicated field trials. The substituted triticales bred in the mid-1970s did tolerate a level of Al in solution comparable to the Al-tolerant wheats as was previously noted by Aniol et al. (1980). However, the substituted triticales were relatively poor performers on very acid soils, presumably due to a lack of additional rye Al-tolerance genes (Camargo & Felicio, 1984).

The root growth observed when rye germplasm was grown in Al-containing solutions is indicative of its known ability to grow on acid soils. The fast growing root system of rye is a particular trait of the species that might not necessarily relate to better Al tolerance. The differences in root elongation and RTI within the four ryes indicated that variation for Al tolerance exists within the small rye group analyzed and that further Al-tolerance improvement in rye as a species might be realized by intercrossing, screening, and selecting rye in hydroponic solutions containing Al.

Unfortunately, the expression of rye Al-tolerance genes in triticale is thought to be partially suppressed by the interaction with the wheat genetic background. Evidence from rye addition and substitution lines into Al-sensitive wheats 'Anza' and 'Chinese Spring'

demonstrated that genes on certain wheat chromosomes affected rye gene expression for Al tolerance (Aniol & Gustafson, 1984). Individual wheat chromosome arms were also shown to have a marked effect on rye Al-tolerance gene expression (Gustafson & Ross, 1990). Taken together, the data suggest that the Al-tolerance in wheat-rye hybrids is influenced by the genetic composition of both the wheat and rye parents (Gustafson & Ross, 1990). The significantly improved Al-tolerance levels observed in the advanced triticale lines of the present study indicated that the expression limitations on rye Al-tolerance gene expression can be progressively improved by breeding, whereas in wheat alone there appears to be no additional genes for further improvement.

It would be of value to investigate further the observation that longer roots and higher RTI values of complete triticales were related to different genetic mechanisms in triticale (Rajaram et al., 1991). If so, it may be possible to make significant improvements in the adaptation of triticale to acid soils not currently under cultivation. If triticales can be improved, then it should also be possible to transfer this rye genetic system for improved Al-tolerance into wheat backgrounds via chromosome substitutions and translocations, thus making an improvement in Al tolerance beyond that observed in the wheats BH 1146 and 'Atlas 66'.

New cultivars with improved Al tolerance will make wheat production on acid soils possible and more cost effective, thus providing an alternative to the current possibilities for improving production where acid soils exist. The current screening procedure to identify genotypes with improved acid-soil performance is rapid, cheap, and very useful for wheat and triticale breeding programs. Triticale breeders in Brazil appear to be selecting for additional Al tolerance from the rye parent, which suggests that by utilizing rye, Al-tolerance levels can be improved along with improvement of other agronomic traits. Since liming is becoming more expensive, Al-tolerant triticale and wheat cultivars will be preferred by farmers in the future as a stable means of increasing cereal production in many areas of the world where marginal soils low in pH and high in Al exist.

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